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Trends in the abundance and distribution of sea otters (*Enhydra lutris*) in British Columbia updated with 2013 survey results

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

In 2013 the BC sea otter population had a minimum of 6,754 sea otters: 5,612 sea otters were counted in the Vancouver Island region and 1,142 sea otters in the central mainland coast region. The population has continued to grow and expand its range since the last survey, demonstrating population growth patterns that are typical among recovering sea otter populations. In the Vancouver Island region, which encompasses the west and north coast of Vancouver Island as well as Queen Charlotte Strait, annual growth was estimated regionally to have been 6.8% year^{-1} (*SE* = 1.20) during 2004 to 2008 and 7.2% year^{-1} (*SE* = 1.05) from 2009 to 2013. These rates are similar but slightly lower than previous estimates for the period 1995 to 2008. They reflect density dependent growth along some parts of Vancouver Island where the sea otter population is approaching carrying capacity. This trend was detected in this assessment by fitting growth models to sub-regional data sets and estimating growth rates over shorter time intervals than has been done previously. On the central BC mainland coast, growth averaged 4.2% year^{-1} (*SE* = 1.62) during 2004 to 2008 reflecting density dependent growth in the longest occupied sub-region. However the contribution of exponential growth in sub-regions where range expansion was first noted in 2007 and 2008 contributed to a much higher regional rate of 12.6% year^{-1} (*SE* = 1.65) for the most recent five-years 2009 to 2013.

Tendances relatives à l'abondance et à la répartition de la loutre de mer (*Enhydra lutris*) en Colombie-Britannique mises à jour d'après les résultats du relevé de 2013

RÉSUMÉ

En 2013, la population de loutres de mer en Colombie-Britannique comptait au moins 6 754 individus : 5 612 loutres de mer ont été dénombrées dans la région de l'île de Vancouver et 1 142 sur la côte centrale de la province. La population a continué de croître et étendu son aire de répartition depuis le dernier relevé, suivant des profils de croissance caractéristiques des populations de loutres de mer en voie de rétablissement. Dans la région de l'île de Vancouver, qui englobe les côtes ouest et nord de l'île de Vancouver ainsi que le détroit de la Reine-Charlotte, la croissance annuelle estimée à l'échelle régionale était de 6,8 % par année^{-1} (ET = 1,20) de 2004 à 2008 et de 7,2 % par année^{-1} (ET = 1,05) de 2009 à 2013. Ces taux sont similaires, quoique légèrement inférieurs, aux estimations précédentes pour la période s'étendant de 1995 à 2008. Ils reflètent la dépendance à la densité à certains endroits sur le littoral de l'île de Vancouver là où la population se rapproche de sa capacité de charge. Cette tendance a été observée dans cette évaluation en ajustant les modèles de croissance aux ensembles de données sous-régionales et en estimant les taux de croissance pour des intervalles plus courts que ce qui avait été fait auparavant. Sur la côte centrale de la Colombie-Britannique, la croissance moyenne était de 4,2 % par année^{-1} (ET = 1,62) de 2004 à 2008, situation qui témoigne de la dépendance à la densité dans la plus longue sous-région fréquentée par la loutre de mer. Toutefois, la croissance exponentielle dans les sous-régions où l'élargissement de l'aire de répartition a été noté pour la première fois en 2007 et 2008 a contribué à un taux de croissance régional beaucoup plus élevé de 12,6 % par année^{-1} (ET = 1,65) au cours des cinq dernières années (2009 à 2013).

INTRODUCTION

Knowledge of population abundance and growth trends is essential for conservation of sea otters in British Columbia. Canada's sea otter population includes descendants of animals reintroduced to Checleset Bay on the west coast of Vancouver Island from Alaska during three translocation efforts in 1969, 1970 and 1972 (Bigg and MacAskie 1978). The original population is thought to have been extirpated by 1930 as a result of commercial hunting for pelts that had begun with the maritime fur trade along the west coast of North America beginning in the late 1700's (Nichol 2015). Following successful reintroduction of 89 animals from Alaska, the BC sea otter population was first surveyed to estimate abundance in 1977 and subsequently at 1 - 3 year intervals thereafter, although not all the range was surveyed. In 1989 a group of sea otters were reported from the Goose Island Group on the central mainland coast signifying the establishment of sea otters in the area (BC Parks 1995[1]).

From 1977 to 1988, surveys were made mostly from fixed-wing aircraft (Bigg and MacAskie 1978; Morris et al. 1981; MacAskie 1987). Since 1988 a standardized survey approach has been used to survey by small boat. The method is a direct count of sea otters in their known range whereby the range is surveyed by the same routes, using consistent methods with the same observers or observers with comparable experience from survey to survey. The precision of replicate counts obtained by this survey method in *Good* to *Excellent* survey conditions has previously been estimated to be (CV = 7-12%) indicating that a high degree of precision is achievable (Watson *et al.* 1997; Nichol *et al.* 2005). The resulting counts provide an index of abundance and data with which to calculate trends in population growth. In 2001 the method was modified to include helicopters as an alternative platform to facilitate coverage of large and remote coastal areas (Nichol *et al.* 2005). Direct count approaches are used to obtain population index counts and estimate average growth rates in the known range in Washington State and California as well, but they use fixed wing aircraft and shore counts (Jameson and Jeffries 2014; USGS 2014).

Sea otter populations can be successfully surveyed using these methods because of specific characteristics of sea otter behaviour and biology that make them predictable in distribution. Sea otters live in nearshore coastal habitats and are most commonly found within the 40-metre depth contour. The sea otter feeds on benthic invertebrates which they collect from the sea floor by diving. Sea otters require frequent access to foraging habitat in subtidal and intertidal habitat and most foraging dives occur in depths of 30 metres or less (Reidman and Estes 1990; Bodkin *et al.* 2004; Lafferty and Tinker 2014). The extent of sea otter habitat is thus set by the limits of their preferred foraging depth with the result that most sea otters are found within 1 to 2 km of shore unless shallow areas extend further offshore (Reidman and Estes 1990; Bodkin *et al.* 2004).

Within this relatively narrow nearshore band, sea otters are non-migratory and occupy small overlapping home ranges throughout their lives. Territorial male home ranges can be 4 to 11 km^2, and female home ranges vary from a few to 24 km^2 (Garshelis and Garshelis, 1984; Ralls *et al.* 1988; Jameson, 1989). The sea otter is gregarious and spends a considerable amount of its time resting in floating aggregations called rafts, that may number over 200 animals. Sea otters segregate by sex and form male rafts and female and pup rafts. Rafts form habitually in the same location and are often associated with particular reefs and kelp beds. The aggregating behaviour of sea otters results in a clumped distribution that is probably also associated with

[1] BC Parks. 1995. Sea Otter Management Plan, for Hakai Recreation Area. [Unpublished reported prepared by J.C. Watson for] British Columbia Ministry of Water Land and Air Protection, Parks and Protected Areas Branch.

habitat characteristics. In British Columbia, sea otters generally occupy coastal areas exposed to the open Pacific as opposed to protected water ways. Along the exposed coast, sea otters are found particularly along shorelines characterized by jagged coastlines with clusters of small islets and reefs and shallow variable depths (Gregr *et al.* 2008).

The distribution of rafts of sea otters can be an indicator of range expansion events in growing populations. The periphery, or frontal edge of the occupied range, tends to be occupied by male rafts. Range expansion in a growing population is triggered by population density in the occupied range. The appearance of a male raft in a previously unoccupied area signifies the first phase of range expansion. In subsequent years, rafts of females form in the new area (Garshelis *et al.* 1984; Jameson 1989; Lafferty and Tinker 2014).

At the time of sea otter re-introductions to British Columbia, sea otters had also been reintroduced to Washington State and to Southeast Alaska with success (Jameson *et al.* 1982). These reintroduced populations, including the one in BC, grew rapidly in the early years at rates of 17-25% per year, the maximum rate possible for the species in the absence of density dependent factors (Estes 1990). The reason for these high rates during the early phase was likely a result of abundant invertebrate prey which had increased in the absence of sea otters. Sea otter populations are regulated by food through density dependent processes that result in elevated rates of mortality, particularly juvenile mortality, as food becomes limiting in an area (Estes 1990; Thometz *et al.* 2014). The minimum population estimate for the Washington State population in 2013 was 1,272 animals with growth since 1989 of 7.6% year^{-1} whereas growth from 1978 to 1987 was estimated to be 17.2% year^{-1} (Estes 1990; Jameson and Jeffries 2014). In Southeast Alaska, an aerial strip transect method is used (Bodkin and Udevitz 1999). The most recent population estimate from surveys (2005 to 2012) is 25,712 otters (based on a total of five sub-region estimates with CVs ranging from 0.18 to 0.38) with an annual growth rate of 12 to 14% year^{-1} (USFW 2014). The growth rate in Southeast Alaska estimated from 1975 to 1987 is 17.6% year^{-1} (Estes 1990).

Following reintroduction of sea otters into Checleset Bay (in 1969-72), the population grew but until 1987 was found in only two locations along the west coast of Vancouver Island, Checleset Bay and off Nootka Island (Bigg and MacAskie 1978). By 1995, the population had increased to 1,522 otters and was distributed along Vancouver Island from Estevan Point to the entrance of Quatsino Sound (Watson *et al.* 1997). By 2004 the population was distributed from Clayoquot Sound to the northwestern edge of Queen Charlotte Strait. On the central mainland coast the population had expanded northeast ward from the Goose Group to the edge of Milbanke Sound by 2001 and to Aristazabal Island by 2008 (Nichol *et al.* 2009). By 2008 when a range-wide survey was completed, the sea otter population in BC included a minimum of 4,712 sea otters, with 4,110 occupying the Vancouver Island region and 602 the central mainland coast region (Nichol *et al.* 2009). The growth rate on Vancouver Island was estimated to be 19.0% year^{-1} from 1977 to 1995 but slowed thereafter to 8.4% year^{-1} to 2008. Population growth on the central mainland coast averaged 11.4% year^{-1} from 1990 to 2008.

In 2013, a range-wide boat survey was completed which encompassed the occupied range on Vancouver Island and the central mainland coast. As well, most of the central mainland coast range was also surveyed in 2011 by boat. In this report, an new index count for 2013 is presented along with population growth rate estimates from within and between the two regions of Vancouver Island and the central mainland coast.

The Terms of Reference specifically for this document are;

- Describe changes in the range of the sea otter in 2013 compared to previous assessments and compared to the historic range and since re-introduction in 1969-72.
- Provide a minimum abundance estimate for the population in 2013,

- Describe changes in abundance that have occurred since 2008, since 1969-72 and compared to historic abundance.
- Estimate the population growth trend to 2013 in total and by area and compare to 2008 and since reintroduction in 1969-72.

To address the specific request above regarding growth trends by area, growth rates were estimated for sub-regions that comprise the Vancouver Island range and the central mainland coast.

METHODS

SURVEY AREA

For the assessment, two regions are defined that encompass all coastal areas surveyed. The Vancouver Island region includes the entire occupied range on Vancouver Island as well as Queen Charlotte Strait and the adjoining portion of the mainland. The Vancouver Island region includes Checleset Bay where sea otters were reintroduced in 1969, 1970 and 1972 and thus where sea otters have been established for the longest period of time (Figure 1). The second region, called the central mainland coast, includes the coastal waters from Calvert Island north to Aristazabal Island. The central mainland coast region includes the Goose Group, where a raft of sea otters was first reported in 1989.

To facilitate systematic survey coverage, the sea otter range within these regions was divided into segments. Segments boundaries are natural breaks such as points of land, or the transition from a sound to an inlet. Segments can typically be surveyed in a day by boat, although some segments delineated in the past now take more than one day to complete because of population growth, as it takes longer to count more otters. Within segments, survey coverage is defined by established survey routes. As of 2013 16 segments comprise the Vancouver Island region and a further six segments comprise the central mainland coast region (Figure 2).

In addition to survey segments, areas adjacent to survey segments or areas from which a report had been received of sea otters were also surveyed to monitor range expansion. Over time new survey segments were added as the sea otter range expanded. The marine mammal program at the Pacific Biological Station solicits reports of sea otter sightings from other researchers, fisheries patrol vessel personnel, fisheries enforcement officers, coastal residents and fishermen to help identify range expansion events and thereby define the extent of survey coverage needed during the range-wide surveys completed at five year intervals. Since 2001, surveys have also been made periodically in inlets adjacent to several occupied areas such as Clayoquot Sound, Checleset Bay, Esperanza Inlet and Quatsino Sound on Vancouver Island, to ascertain whether there has been unreported movement of otters into these areas.

Following the survey of new areas, only those in which a raft of sea otters was observed during a survey were considered occupied. This criterion is used, for consistency, to identify range expansion events. Although single sea otters are encountered and reported outside the occupied range occasionally throughout BC (Ford 2014), the presence of rafts during spring or summer – which is when sea otter surveys are undertaken – is used to define range of occupation. During winter months it is not uncommon for a raft of sea otters to make irregular appearances in new areas, but consistent occupation of the new area may take several years and coincides with observed occupation during spring and summer. Survey coverage in 2013, including new areas surveyed in 2013, is shown in Figure 1.

SURVEY METHOD

Survey routes within segments followed the coastline and included coverage of waters around all islets and reefs; habitats typically occupied by sea otters. Survey routes were recorded by interfacing a GPS device with navigation software (Nobeltec Visual Navigation Suite, Nobeltec Corporation, or Navionics) on a laptop or iPad. Small boat surveys were conducted by two or three observers and one boat driver. The small vessels used were 5.5-metre welded aluminum boats or 6.5-metre rigid hull inflatable boats. Observers searched for and counted sea otters on either side as well as forward of the boat as the vessel proceeded along the course. The number of otters sighted was recorded and their location was approximated as the position of the boat at the time of the sighting. Locations of rafts were further refined by examining the marine features on the chart and the boat's position. The boat traveled at speeds of less than 10 knots (18.5 km/hour). Speed was altered as required and the boat was stopped frequently to search complex areas with binoculars and to obtain counts of the number of animals in rafts.

During small boat surveys, rafts of sea otters were counted using 7X50 binoculars and 14X40 stabilized binoculars. Female rafts were distinguished from male rafts by the presence of pups. Rafts were counted by all observers. Each person assessed the raft size independently, making several counts when possible and then compared counts. The final count accepted was the best overall repeatable count and this value was often among the higher of the initial counts, because counts were made as the boat and otters rose and fell in the ground swell and high counts were obtained when an observer achieved an unobstructed view of the sea otter raft.

Additional counts were collected in 2009 and 2013 by observation from a large ship following a report of a raft of sea otters (G. Ellis pers. com. 2008) on Cook Bank, offshore of the Cape Scott to Hope Island segment of northern Vancouver Island. To survey the area, two observers collected sightings from the top viewing deck in 2013, (10 m above the water), and from the bridge in 2009 (7.5 m above the water) of the Canadian Coast Guard vessel *Tanu* as it made a single transit travelling parallel to the coast at 10 knots. The observers scanned the ocean on either side of the vessel and the position of otter sightings were approximated as the position of the ship at the time of the sighting.

Sea and weather conditions were recorded during surveys and were categorized as follows. *Good* to *Excellent* survey conditions existed when sea state ranged from flat calm (Beaufort 0) to swells up to 1 m and wind speeds less than 10 knots (18 km/hr) (Beaufort 3). *Fair* conditions were defined generally as seas 1 to 1.5 m or when wind speeds ranged from 10 to 15 knots (28 km/hr) (Beaufort 4). *Poor* conditions were generally defined as seas greater than 1.5 m or wind speeds greater than 15 knots (28 km/hr). High overcast created ideal lighting conditions due to reduced sun glare. Surveys did not commence in *Poor* conditions or when visibility was obscured particularly through binoculars, e.g., by rain or fog. Although *Good* to *Excellent* conditions were sought, sea states often changed during the course of a survey. If conditions deteriorated, the survey was repeated at a later date whenever possible. All surveys to document minimum population size, distribution and range of occupation have been carried out from May through early September since 2004. In earlier years surveys were conducted between April and September. Further details about the survey methodology including details about the methodology adapted for use from helicopter (some surveys 2001 to 2004) are described in Nichol *et al.* (2005).

ANALYTICAL METHODS

Survey segment counts made in 2013 and counts from new areas occupied by rafts of sea otters were summed to obtain a minimum population size for 2013 for the Vancouver Island region and the central mainland coast region. To estimate growth rates in the population over time, we first fit growth models to annual survey data on a sub-regional basis. Survey segments were grouped into sub-regions according to similarity in years of occupation and contiguous

geography. Annual survey counts from the member segments were summed. Grouping survey segments into sub-regions also achieved a minimum of three years of survey effort over a five-year period, which was needed to fit models. The sub-regions do not represent distinct population units, but this approach made it possible to assess growth trends on a smaller scale and allowed incorporation of much more survey data from years between the range wide surveys during which only portions of the sea otter range were surveyed. The 16 segments that comprise the Vancouver Island region were grouped into seven sub-regions. The six segments in the central mainland coast region were grouped into three sub-regions. To obtained a regional estimate of growth rate, that could be compared with the regional growth rate estimates from previous assessments, we combined the sub-regional model estimates.

The time series for each segment in a sub-region was inspected for gaps and for multiple surveys. If more than one survey had been made in a year in a segment, the survey made under the best conditions, which generally yielded the higher count, was selected. If a survey had not been completed in a segment in a year, then that year was excluded from sub-region time series, unless the missing count would make up < 20% of the total sub-region count. In these instances we estimated the number of animals in a missed segment by interpolation using the exponential equation that best fit a maximum of four counts preceding and/or succeeding the missing count. Only four interpolated values were used among all sub-regions and years.

In this assessment, we fit two alternative growth models to the time series available for each sub-region using Maximum Likelihood methods. All calculations were performed using MatLab R2014a. The models evaluated were for exponential and for logistic population growth with discrete 1-year time steps, described by the following equations:

(1) $$exponential: N_{pred,t} = N_{pred,t-1} \cdot e^{r}$$

(2) $$logistic: N_{pred,t} = N_{pred,t-1} \cdot e^{r\left(1-\left[N_{pred,t-1}/K\right]\right)}$$

where $N_{pred,t}$ is the predicted abundance at time t, and r (the intrinsic or instantaneous rate of growth) and K (carrying capacity) are fitted parameters. The solution to both models required one additional estimated parameter, N_0, the initial abundance at year 0 (defined as the year before the first available count for that subregion). Model fitting was accomplished using unconstrained numeric optimization to maximize the following likelihood function (Hilborn and Mangel 1997) which compared observed to predicted counts:

(3) $$\ell(N_{obs} \mid Model_j, r_i, k_i, N_{0,i}) = \frac{1}{\sqrt{2 \cdot \pi \cdot \sigma^2}} \cdot e^{\left(\frac{-(N_{obs}-N_{pred})^2}{2 \cdot \sigma^2}\right)}$$

where N_{obs} is the vector of observed counts and N_{pred} is the vector of predicted counts, given a particular model and set of parameter estimates (r_i, K_i and $N_{0,i}$). The parameter σ^2 represents the variance term, solved for by iterative re-weighting (following Pascual et al. 1997). We thus assume that deviations between observed and model-predicted counts were normally distributed with mean 0 and standard deviation σ, and thus we assume that deviations primarily reflect observer error rather than process error (Hilborn and Mangel 1997; Tinker et al 2006).

We used the Akaike Information Criterion (AIC) to select the most parsimonious of the two models for each sub-region, and calculated R^2 to evaluate goodness of fit of the selected model. For each sub-region we report maximum likelihood estimates and associated standard errors for

r and K (the latter is reported only for those sub-regions where logistic growth was the best supported model), and also for σ (expressed as a coefficient of variation, CV = σ/N). Additionally, for each sub-region we report the estimated finite rate of growth (r_d) for the most recent 5-year period (2009-2013) and for the previous 5-year period (2004-2008). Note that $r_{d,t}$ is a measure of the average realized rate of population growth over some defined interval (expressed in units of annual percent increase in population size) and thus differs from the model parameter r (the instantaneous rate of growth as N $\rightarrow$0). We calculated $r_{d,t}$ as:

$$r_{d,t} = 100\left(\left[N_{pred,t} \Big/ N_{pred,t-4}\right]^{\frac{1}{4}} - 1\right) \quad (4)$$

We calculated a standard error for $r_{d,t}$ using a resampling approach, whereby we generated 20,000 random parameter sets for equation 1 or 2 (as appropriate), used these to solve equation 4, and calculated the standard deviation of $r_{d,t}$ across all iterations. Parameter sets for each iteration were drawn from a multivariate random normal distribution with mean values equal to the maximum likelihood estimates and variance-covariance matrix calculated as the inverse of the hessian matrix derived from the maximum likelihood solution of equation 1 or 2. We also report $r_{d,t}$ for the entire region (i.e., by summing the annual expected counts derived from the best fit model for each sub-regions).

Maps

Map figures were produced using ArcMap 10.2.2. Survey effort is represented by kilometres of survey transect and sea otter distribution by the location of sightings in 2008 and in 2013. Numbers of sea otters per sighting are not depicted on the map figures.

RESULTS

REGIONAL POPULATION ESTIMATES AND GROWTH RATES

Surveys of the Vancouver Island region were made from May 13 to August 25, 2013. The central mainland coast region was surveyed from May 9 to May 21, 2013 and from June 10 to June 22, 2011. Survey conditions during both 2013 and 2008 (for comparison) are presented in Table 1. Range expansion has taken place since 2008 in both regions (Figure 3). The geographic distribution of survey effort and otter sightings in 2013 is presented in Figures 4, 5, and 6 and in 2008 in Figures 7, 8 and 9. Sea otters were observed singly and in groupings of up to 250 animals. Approximately half of the sea otters were observed in rafts of more than 30 animals, the other half in smaller groups and as single animals (Figure 10).

Vancouver Island Region

A total of 5,612 sea otters were counted in the Vancouver Island region in 2013 (Table 2). The finite rate of growth for the region was 7.2% year^{-1} (*SE* = 1.05) over the period of 2009 to 2013 inclusive. During the five-year period 2004 to 2008, the finite rate of growth was 6.8% (*SE* = 1.20). These estimates are not significantly different from each other (Figure 11).

Central Mainland Coast Region

A total of 1,142 sea otters were counted in 2013. In 2011, 757 sea otters were counted although the Aristazabal Island segment and the Seaforth Channel to Ivory Island and Lady Douglas Island segment were not surveyed in that year. The finite rate of growth was estimate

to be 12.6% year^{-1} (*SE* = 1.65) from 2009 to 2013 and 4.2% year^{-1} (*SE* = 1.62) from 2004 to 2008 (Figure 12).

SUB-REGIONAL ANNUAL RATES OF INCREASE AND RANGE EXPANSION

Vancouver Island Region

Rates of growth among sub-regions generally corresponded inversely with years of occupation and with the proportion of the total population in sub-regions. Near the centre of the range, where the population has been established for the longest period of time (sub-regions 5 and 6) the annual rates of increase were the lowest of all the sub-regions on Vancouver Islands in both the 2004 to 2008 and the 2009 to 2013 periods. In 2009 to 2013 the growth rate in sub-region 5 was 2.6% year^{-1} (*SE* = 0.66), and in sub-region 6, 2.5% year^{-1} (*SE* = 1.23). A logistic population growth model, best describes the pattern of growth in these sub-regions where half of all sea otters on Vancouver Island occur. Rates of annual increase are higher among sub-regions to the south and to the north and three northern sub-region most recently occupied had average annual rates of increase during 2009 to 2013 that exceeded 20% year $^{-1}$ (Figure 13 and Table 3).

Since 2008 range expansion events in the Vancouver Island region have taken place mainly in the north in Queen Charlotte Strait (see Figures 3, 4, 7). The presence of a raft of male sea otters amongst an island group in Queen Charlotte Strait east of Hope Island was recorded on surveys in 2009 and 2010. A raft of males was observed along the mainland shore of Queen Charlotte Strait in 2013 and another raft was observed north of Queen Charlotte Strait in Smith Sound in 2013. In contrast there has been little evidence of range expansion elsewhere, although sea otters expanded into Esperanza Inlet in 2008 and since then rafts of male sea otters have been observed in adjoining Tahsis Inlet (R. Dunlop, biologist for Nuu-chah-nulth Tribal Council, Gold River, BC pers. comm. 2013) indicating that sea otters are now established around all of Nootka Island. An example of range expansion and subsequent occupation and population growth is illustrated in Figure 14 with survey data from the Catala Island segment. Initial immigration of a raft of male sea otters in 1992 was followed, in subsequent years, by population growth as females established in the area.

Central Mainland Coast

Sub-region 10 which includes the Goose Group segment and the McMullin Group to Cape Mark segment has been occupied for longer than any other part of the central coast range. More than half of the otters counted on the central mainland coast in 2013 occurred in this sub-region. Growth in this sub-region was minimal and similar to the longest occupied sub-regions of Vancouver Island, with an annual rate of increase in 2009 to 2013 of 2.4% year^{-1} (*SE* = 1.33). In contrast the sub-region to the north that includes Aristazabal Island (sub-region 8) and sub-region 9 to the east, both of which have only been occupied since no earlier than 2007 have high annual rates in excess of R_{max} (Figure 15 and Table 4).

Range expansion to Calvert Island occurred after the surveys were completed in June 2013 (L Honka, M.Sc. student, School of Resource and Environmental Management, Simon Fraser University pers. comm. 2013). Although not observed during surveys, a large raft of male sea otters arrived during summer and therefore the west side of Calvert Island was considered occupied in 2013. Elsewhere in sub-regions 9 rafts of females were recorded by 2011.

DISCUSSION

The sea otter population in British Columbia has continued to grow and its distribution increase demonstrating population growth patterns that are typical of recovering sea otter populations. Annual growth rates were much lower in long occupied sub-regions of Vancouver Island and the central mainland coast than in more recently occupied sub-regions reflecting density dependence, whereby growth approaches zero as population size approaches carrying capacity (*K*). Growth rates in more recently occupied sub-regions were higher and in many cases higher than R_{max} estimates for the species, indicating that immigration was an additional factor (Estes 1990).

The survey methodology provides an index of abundance assumed to represent a constant proportion of the population. Sea otters are a non-migratory nearshore species. They exhibit raft site fidelity and occupy small coastal home ranges over their lives. These attributes contribute to the success of the direct count method. Similar methods have been used to assess trends in population size and growth in Washington State and California (Jameson and Jeffries 2014; USGS 2014). Data collected with this survey method in BC also provide detailed, relatively fine-scale information about the distribution of sea otters, locations of rafts by sex and the timing of range expansion events, because parts of the range are surveyed annually in addition to the range wide survey completed at five-year intervals.

A challenge for long-term population survey programs such as this, however, is maintaining a consistent level of effort as the population increases and expands its range. In response to this challenge the survey method was adapted in the early 2000's for surveys from helicopter, a platform that would allow more rapid coverage of survey segments and thereby more survey coverage per unit time. Counts obtained from boat and from helicopter made in the same survey segment and within the same season produced comparable results. This supported the assertion that counts by the two methods could readily be used together in analysis (Nichol *et al.* 2005). However, helicopter surveys are significantly more expensive and have not been possible in recent years but the challenge of maintaining consistent effort persists.

In 2009 and during the range wide survey in 2013, sea otters were counted from the CCG ship *Tanu* on an offshore transect as well as by small boat along the established inshore route at the north end of Vancouver Island in the Cape Scott to Hope Island segment. The offshore area had not previously been surveyed. The resulting counts are used in the growth rate estimates and in the population index count for 2013 reported here. It is unknown, however, how many sea otters might have been counted in the offshore transect had it been surveyed in earlier years. It will be important to continue to incorporate offshore survey effort over this shallow bank in the future. Small boats are well suited for surveys in shallow rocky nearshore habitat, where a shallow draft and maneuverability are needed. Large ships are better suited for survey of expansive offshore areas because of greater efficiency and stability, and the higher viewing platform provides a wider field of view. Further methodological development is needed though to be able to compare survey results from ships and small boats as was done previous with counts from small boats and helicopters (Nichol *et al.* 2005).

Regional annual growth rate estimates for Vancouver Island and the central mainland coast, as a whole, were generally consistent with previous growth trajectories for the two regions (Nichol *et al.* 2005; 2009). The Vancouver Island regional growth trends for the two recent five-year intervals, 2004 to 2008 and 2009 to 2013 were similar but slightly lower than the 8.4% year $^{-1}$ estimate previously for 1995 to 2008 (Nichol *et al.* 2009). This probably reflects density dependence in growth in the long occupied sub-regions, where logistic population growth models fit best These sub-regional trends were not as well represented in previous assessments that estimated growth from one exponential growth model fitted to the entire region, over a longer time series but with a more limited data set.

The central mainland coast regional growth rate has always been below R_{max} for the species (Nichol *et al.* 2005, 2009). Although it is unclear why this has been the case, it is possible that greater variability in early counts in the time series, when there was less knowledge of the distribution of sea otters in this area, masked an early phase of rapid growth. Previous assessments have noted a poorer fit of the linear regression to central coast counts compared to Vancouver Island counts, which would suggest greater variability among counts. In this assessment, the width of the confidence intervals around the central mainland coast regional growth curve estimates for the entire time series from 1990 to 2013 are wider than those for the Vancouver Island growth curve estimate and therefore continue to reflect this uncertainty.

We detected significantly different annual growth rates on the central mainland coast between the two five-year time periods, 2004 to 2008 and 2009 to 2013. The much higher growth rate estimate in the latter period includes the contribution from two additional sub-regions of the central mainland coast only recently occupied (since 2007). In the previous assessment the average annual growth rate for the entire region based on a single exponential population growth model fit to data from 1990 to 2008 did not capture the sub-regional effects (Nichol *et al.* 2009).

Fitting growth models to sub-regional data sets allowed for use of more years of survey data than in previously assessments. In previous BC sea otter population assessments (e.g., Watson *et al.* 1997; Nichol *et al.* 2005; Nichol *et al.* 2009), a single regional growth rate for each region was estimated from an exponential growth curve, fitting log counts on year (time) in a linear regression analysis fit by least squares (Zar 1984). As such the previous trend analysis was restricted to use of survey data from years in which an entire region (Vancouver Island or central mainland coast) had been surveyed (or ≥ 70% of the region, Nichol *et al.* 2005, 2009) (see Table 2). This meant excluding many years of survey effort in which only some segments had been surveyed. Fitting growth models to sub-regional data sets has allowed us to use survey data collected during the five years between 1995 and 2001, and the seven years between 2004 and 2013. The result has been a more detailed assessment of the pattern of sea otter population growth in BC.

Although sub-regions do not represent distinct population units, analysis at this level serves to better illustrate the process of sea otter population growth that is a result of demographic processes and range expansion events. Sea otter populations are limited by the availability of food. Growth in the population is a result of births and deaths, measurable on an annual basis, but also as a result of immigration and emigration, which manifest as range expansion events that are detected at longer and irregular intervals. Although food limitations result in density dependent population growth and range expansion, the timing of range expansion events is influenced by social dynamics, the distance from occupied areas to suitable new habitat and the quality of habitat (Tinker *et al.* 2008; Lafferty and Tinker 2014). Gregr *et al.* (2008) modelled habitat complexity (a proxy for habitat quality for sea otters) along the west coast of Vancouver Island from the southern tip of Vancouver Island to a point to the west of Hope Island, and identified habitat areas of similar complexity to those in Checleset Bay, Mission Group and Kyuquot Sound, the areas that comprise the longest occupied sub-region (sub-region 5) in our assessment. Within this study area the results suggested that there may be less similarly complex habitat south of Estevan Point to Clayoquot Sound, (although lots of habitat in Clayoquot Sound) and less complex habitat from Quatsino Sound north. Thus if habitat quality and distribution influences range expansion, then this may partly explain the distribution of sea otters amongst the sub-regions. In other words, the quantity and quality of "good" habitat may be lower outside the two sub-regions where most of the otters are found and this slowed the process of range expansion. Presumably this could change in the future as the population expands further into different habitat which might involve "good" areas.

Annual growth rates during the period 2009 to 2013 were generally at or above R_{max} in recently occupied sub-regions in both the Vancouver Island region and the central mainland coast

region, with the exception of the most southerly sub-region on Vancouver Island (sub-region 7). In sub-region 7 of Vancouver Island that includes Clayoquot Sound, the rate of annual increase from 2004 to 2013, (8.9% year^{-1}, *SE* = 1.82) although higher than the regional rate for Vancouver Island, seems low in an area that should represent the expanding southern edge of the range and an area that according to habitat modelling should have a lot of suitable habitat (Gregr *et al.* 2008). Range expansion by males into Clayoquot Sound was recorded in 2004 but rafts of females were first observed in 2010, suggesting as much as a six-year interval between range expansion by males and the arrival by females.

In contrast, annual rates of increase in the three most northern sub-regions of Vancouver Island were above R_{max}. In sub-region 2 (Cape Scott to Hope Island), for example, the rate of increase estimated from 2004 to 2013 is attributable to increasing numbers of female and pups counted on surveys in the area near Hope Island over the time series. Sea otters observed on the offshore transect in this sub-region in 2013 were spread out foraging, suggesting the offshore area is a productive foraging habitat in close proximity to nearshore rafting areas.

On the central mainland coast, range expansion to Aristazabal Island was first documented on a survey in 2008. This expansion left a geographic gap in the range between the sea otter occupied range on the south side of Milbanke Sound and the occupied range at Aristazabal Island. The gap between these two areas persisted in 2013. Range expansion with gaps between occupied areas in California has been attributed to variation in habitat quality and this is a plausible explanation here as well (Lubina and Levin 1988; Reidman and Estes 1990; Tinker *et al.* 2008). Historical reports of sea otters in inland passages[2] of BC suggests gaps will be filled as prime habitat reaches equilibrium densities. Indeed this may be occurring on Vancouver Island where recent occupation of inlet habitat such as Esperanza Inlet and Quatsino Sound by male rafts since 2001 may be an example of occupation of lesser quality habitat as a trade-off to maintain proximity to females (Nichol *et al.* 2009). On a larger scale, the gap that has persisted between the Vancouver Island region and the central mainland region is now disappearing as sea otters on the central mainland coast have expanded southward to Calvert Island and are also now present in Smith Sound and in Queen Charlotte Strait. In future assessments Vancouver Island and the central mainland coast may need to be viewed as one large region.

The BC sea otter population continues to grow and recover from extirpation in the early part of the 20th century. There are no estimates of the size of the BC sea otter population prior to the maritime fur trade, against which to measure recovery. There are various incomplete historical records that suggest a much larger population than today (Nichol 2015). For example, on Haida Gwaii a single ship trading for less than two months in 1787 amassed 1,821 pelts and another obtained 1,400 sea otters in less than two months in 1791 (Sloan and Dick 2012). From 1790 to 1800 an estimated 10,000 pelts a year were obtained by American vessels alone trading with native people along the coast of northern British Columbia and southeastern Alaska (Dmytryshyn and Crownhart-Vaughan 1976). These statistics suggest that high densities of sea otters were once found not only along Vancouver Island, but also around the islands of Haida Gwaii and along the central and northern mainland BC coast.

Gregr *et al.* (2008) provided several possible estimates of a maximum sea otter population for BC based on a habitat modeling approach. One model for the west coast of Vancouver Island estimated a maximum population of 5,123, (95% CI=3,337–7,104), in high quality habitat and 14,831, (95% CI=9,790–20,751) coast-wide. A second model suggested, 52,459 sea otters coast-wide (95% CI = 34,264–73,489). On the west coast of Vancouver Island, the population

[2] Menzies, naturalist aboard the HMC Discovery in 1790 reports a sighting of a large raft of sea otters in the inland waters of Wright Sound which is north east of Aristazabal Island

count is now within the range of model estimate, but coast-wide the population is far below the estimates of both models.

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TABLES

Table 1. Kilometres of survey effort and survey conditions in 2008 and 2013.

Region	Year	Kilometres	Kilometres surveyed by conditions in all areas surveyed (%)			
			Excellent	Good	Fair	Poor
Vancouver Island	2013	1931	767 (40)	605 (31)	395 (20)	165 (9)
Vancouver Island	2008	1298	196 (15)	732 (56)	287 (22)	83 (6)
Central mainland	2013	963	0	350 (36)	523 (54)	89 (9)
Central mainland	2008	839	157 (19)	313 (37)	320 (38)	46 (6)

Table 2. Sea otter counts by region in years when at least one of the regions was surveyed entirely. Platforms : fixed-wing aircraft- 1, helicopter- 2, small boat- 3. Coast Guard ship - 4. BC Total is only given when both regions were surveyed.*

Year	Vancouver Island	Central Mainland Coast	BC Total	Platforms
1977	70	-	70	1
1978	67	-	67	1
1980	74	-	74	1
1982	116	-	116	1
1984	345	-	345	1,3
1987	370	-	370	1
1988	354	-	354	3
1989	582	-	582	2,3
1990	612	56	668	2,3
1991	486*	104	590	3
1992	801*	168	969	2,3
1993	910	135	1045	3
1994	1188	-	-	3
1995	1423	-	-	3
1996	-	259	-	3
1998	-	429	-	3
2001	2673	507	3180	2,3
2002	2134*	235	2369	2,3
2003	2415	394*	2809	2,3
2004	2765*	420	3185	2,3
2007	-	642	-	3
2008	4110	602	4712	3
2013	5612**	1142	6754	3,4

** includes a few interpolated values for missed counts that total a small proportion of the regional count (see Table 1 in Nichol et al. 2009).*

*** 506 animals counted in sub-region 2 on inshore transect, 396 counted on offshore transect from CCG ship Tanu.*

- region not yet occupied

Source of survey data displayed in Table 2

1977: Bigg and MacAskie 1978

1978: Morris *et al.* 1981

1980-82: Watson et al. 1997

1984: MacAskie 1987

1987-1995: Watson et al. 1997

1996-2013: DFO, J. Watson

Table 3. Model fitting results for sub-regions of Vancouver Island illustrated in Figure 13.

Sub-region	Colour on Figure 14	Date range	Survey years *N*	AIC selected model	2009-2013 annual growth rate (*SE*)	2004-2008 annual growth rate (*SE*)	Instantaneous rate of increase (*SE*)	Estimate of Carrying Capacity *K* (*SE*)	CV	R^2
1. (Queen Charlotte Strait east and Smith Sound)		2009 - 2013	3	Exponential	25.8 (9.46)	--	0.29 (0.12)	--	0.63	0.77
2. (Cape Scott to Hope Island)		2001 - 2013	8	Exponential	29.2 (1.46)	29.12 (1.46)	0.26 (0.01)	--	0.13	0.99
3. (Scott Islands)		2008 - 2013	3	Exponential	23.7 (1.57)	--	0.21 (0.01)	--	0.04	0.99
4. (Brooks Bay, Quatsino Sound, Kains to Cape Scott)		1989 - 2013	14	Logistic (AIC, L = 182.03, E = 185.09)	4.8 (2.87)	9.37 (3.98)	0.20 (0.06)	1197.81 (247.68)	0.39	0.87
5. (Checleset Bay, Mission Group, Kyuquot Sound)		1977 - 2013	32	Logistic (AIC, L = 389.14, E = 409.97)	2.6 (0.66)	4.54 (0.65)	0.14 (0.02)	2083.56 (194.51)	0.22	0.96
6. (Nootka Island Nuchatlitz Inlet, Catala Island, Esperanza Inlet)		1977 - 2013	22	Logistic (AIC, L = 263.65, E = 275.25)	2.5 (1.23)	4.54 (1.75)	0.15 (0.02)	1014.82 (125.49)	0.32	0.92
7. (Hesquiat Peninsula, Clayoquot Sound)		1995 - 2013	9	Exponential	8.9 (1.82)	8.98 (1.82)	0.08 (0.02)	--	0.29	0.77

Table 4. Model fitting results for sub-regions of the central mainland coast, illustrated in Figure 15.

Sub-region	Colour on Figure 15	Date range	Survey years *N*	AIC selected model	2009-2013 annual growth rate (*SE*)	2004-2008 Annual growth rate (*SE*)	Instantaneous rate of increase (*SE*)	Estimate of Carrying Capacity *K* (*SE*)	CV	R^2
8. (Aristazabal Island and Seaforth to Ivory and Lady Douglas Island)		2007 - 2013	3	Exponential	31.9 (0.61)	--	29.85 (0.11)		0.02	0.99
9. (Simmonds Group to Kildidt Sound)		2007 - 2013	4	Exponential	35.1 (3.62)	--	27.57 (2.08)		0.18	0.97
10. (Goose Group, McMullin Group to Cape Mark)		1990 - 2013	13	Logistic (AIC, L = 156.63, E = 157.90)	2.4 (1.33)	4.22 (1.62)	2.01 (1.23)	709.11 (174.61)	0.24	0.84

FIGURES

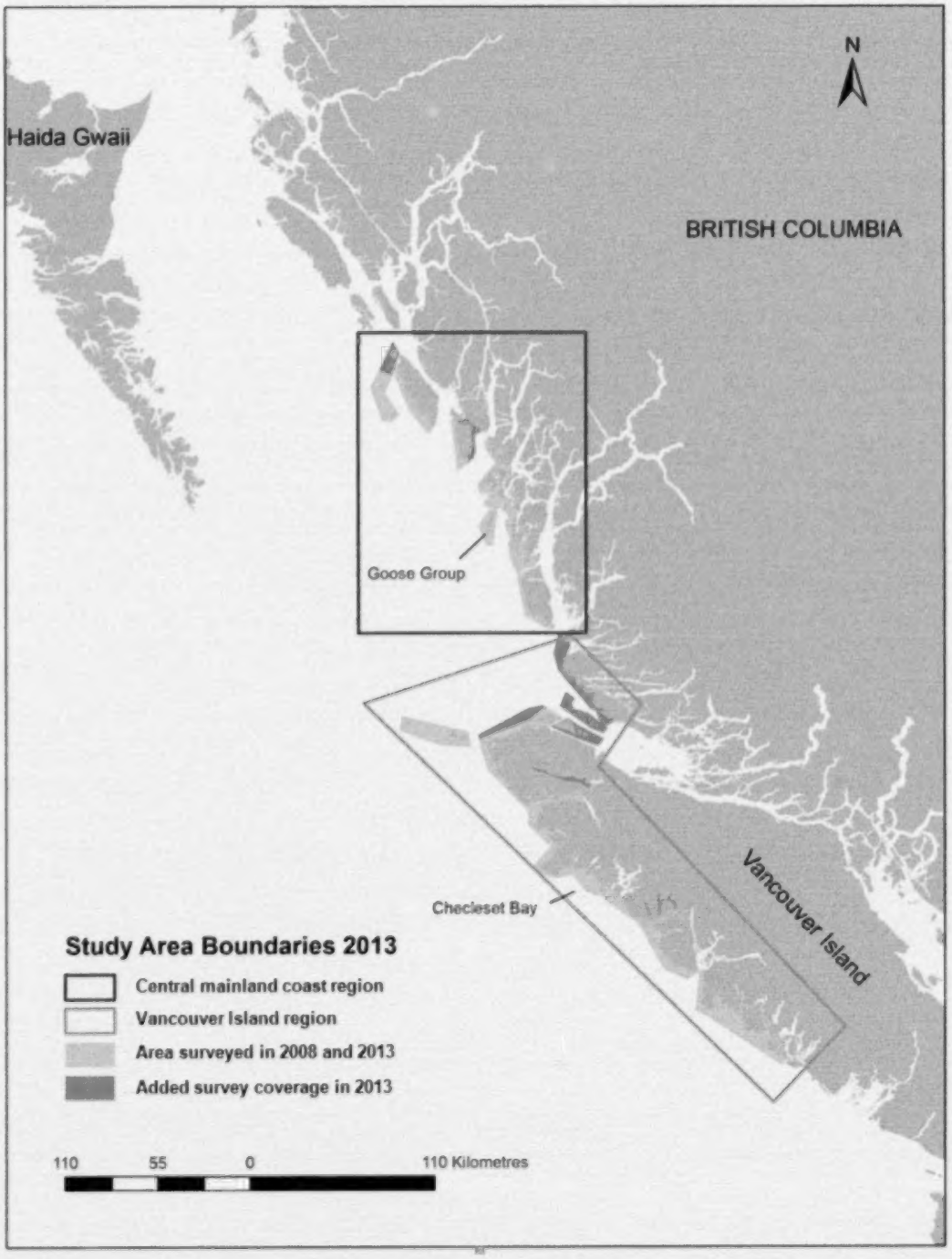


Figure 1. Survey region boundaries and areas within that were surveyed in 2008 and 2013. Checleset Bay site of the original re-introductions 1969-1972. Goose Group where groups of sea otters were first sighted on the central mainland coast in 1989.

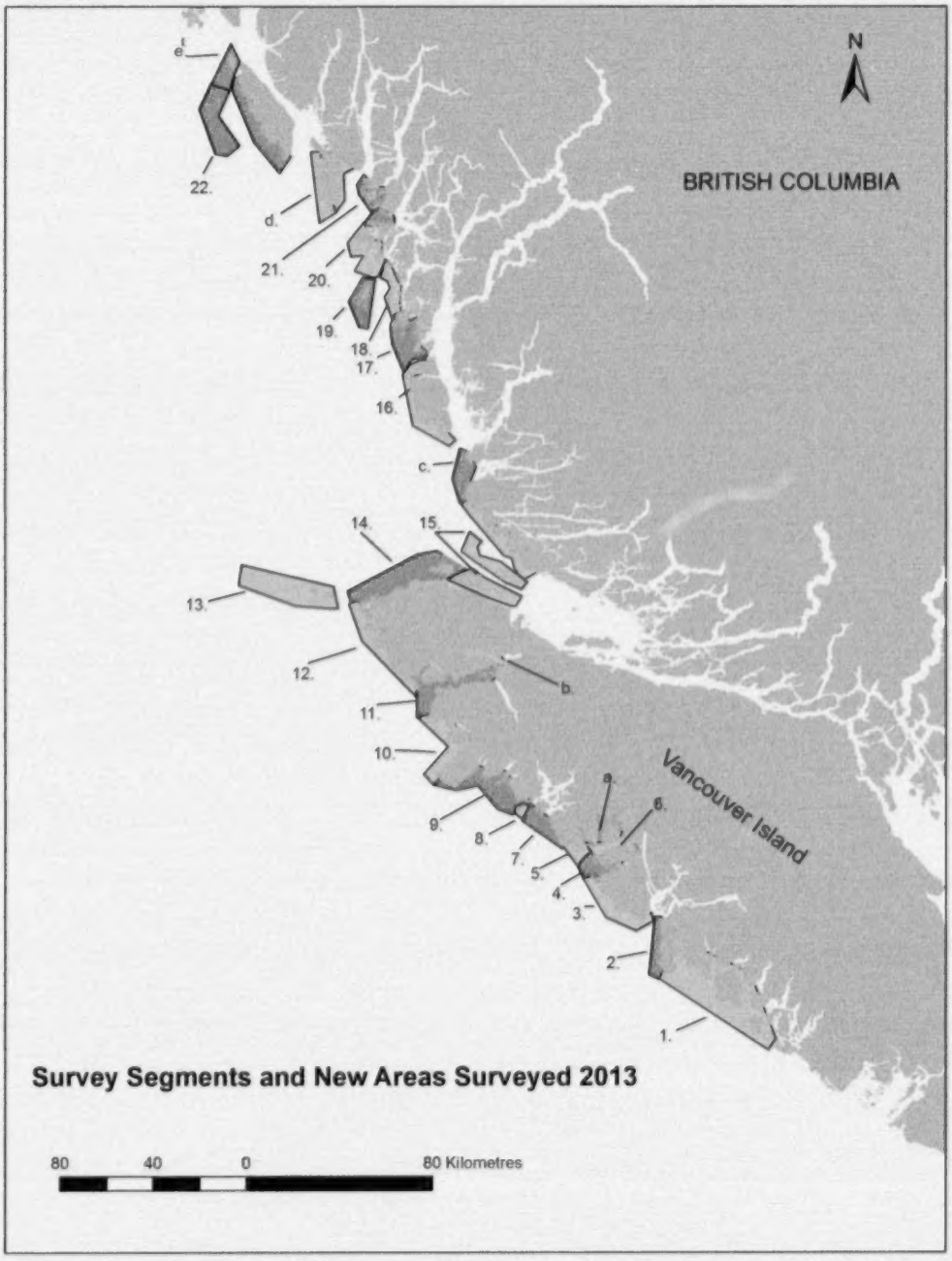


Figure 2. Survey segments and new areas surveyed in 2013. Survey segments: 1. Clayoquot Sound, 2. Hesquiat Peninsula, 3. Nootka Island, 4. Nuchatlitz Inlet, 5. Catala Island, 7. Kyuquot Sound, 6. Esperanza Inlet, 8. Mission Group, 9. Checleset Bay, 10. Brooks Bay, 11. Quatsino Sound, 12. Kains Island to Cape Scott, 13. Scott Islands , 14. Cape Scott to Hope Island, 15. Queen Charlotte Strait east, 16. Calvert Island, 17. Kildidt Sound, 18. Simond Group to Tribal Group, 19. Goose Group, 20. McMullin Group to Cape Mark, 21. Seaforth to Ivory Island and Lady Douglas Island, 22. Aristazabal Island. New areas surveyed to assess range expansion: a. Inlets connected to Esperanza Inlet, b. Holberg Inlet, c. Smith Sound, d. Price Island, e. extension of Aristazabal Island area.

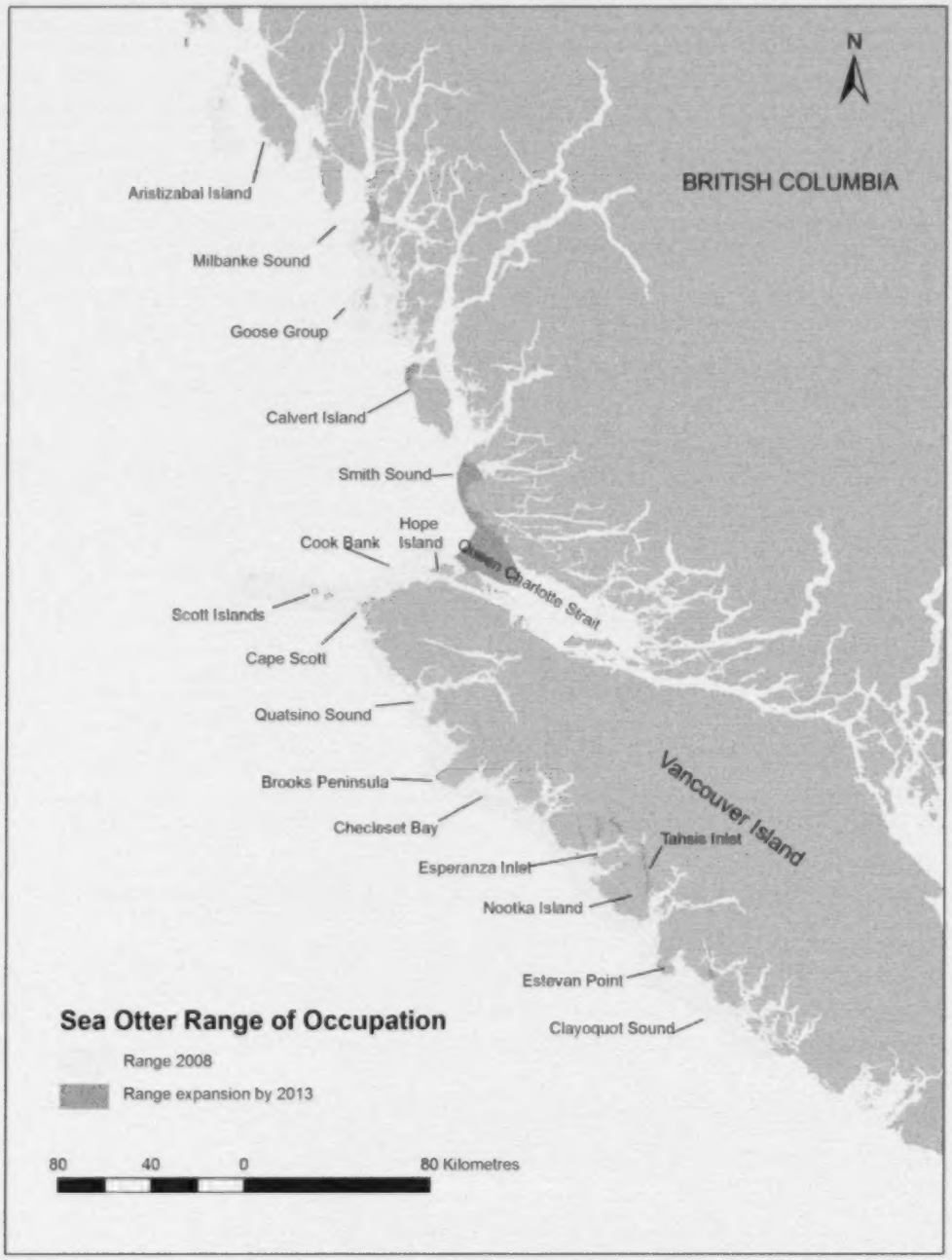


Figure 3. Sea otter range in British Columbia in 2013 and place names mentioned in the text.

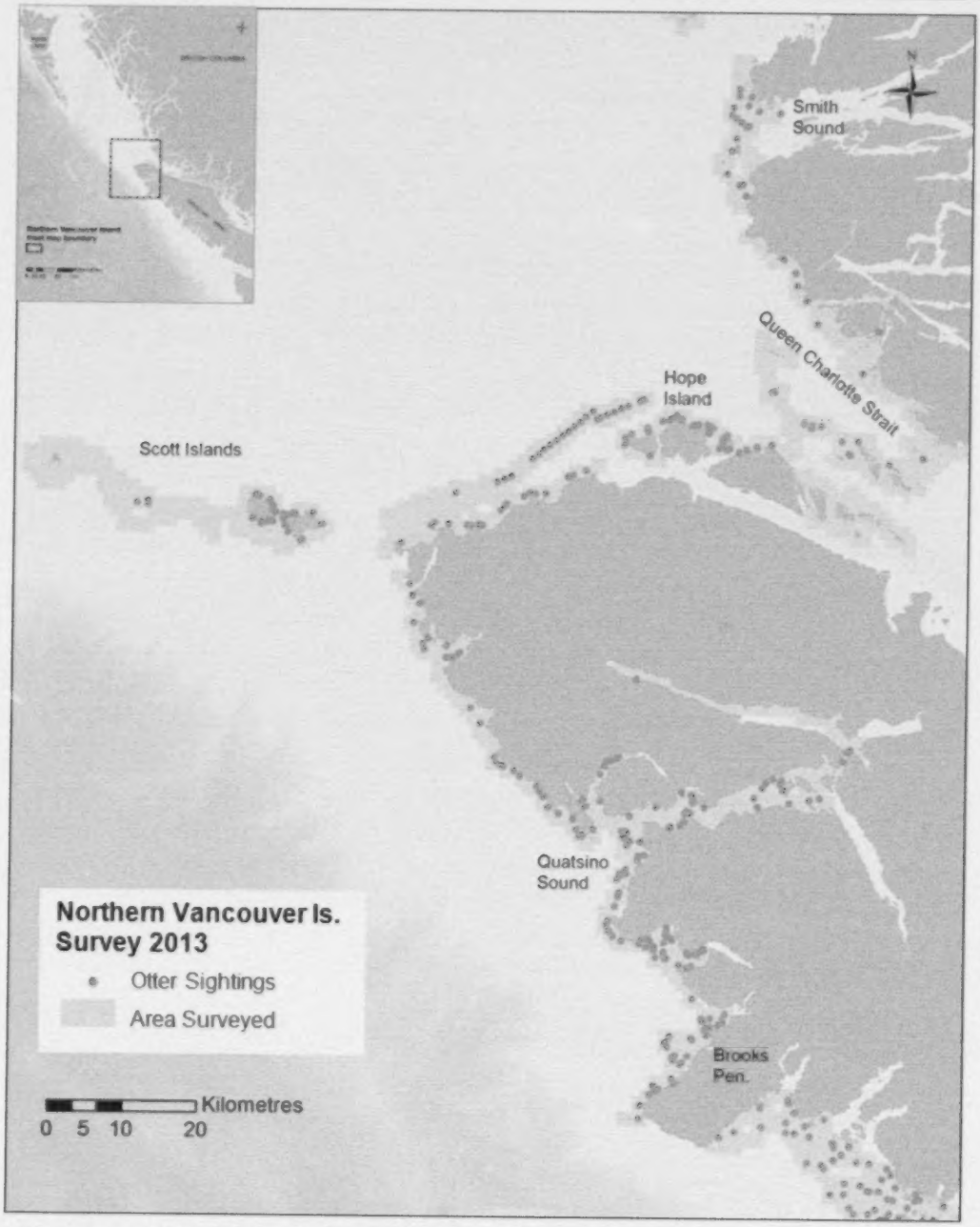


Figure 4. Distribution of sea otter sightings and survey effort on northern Vancouver Island in 2013.

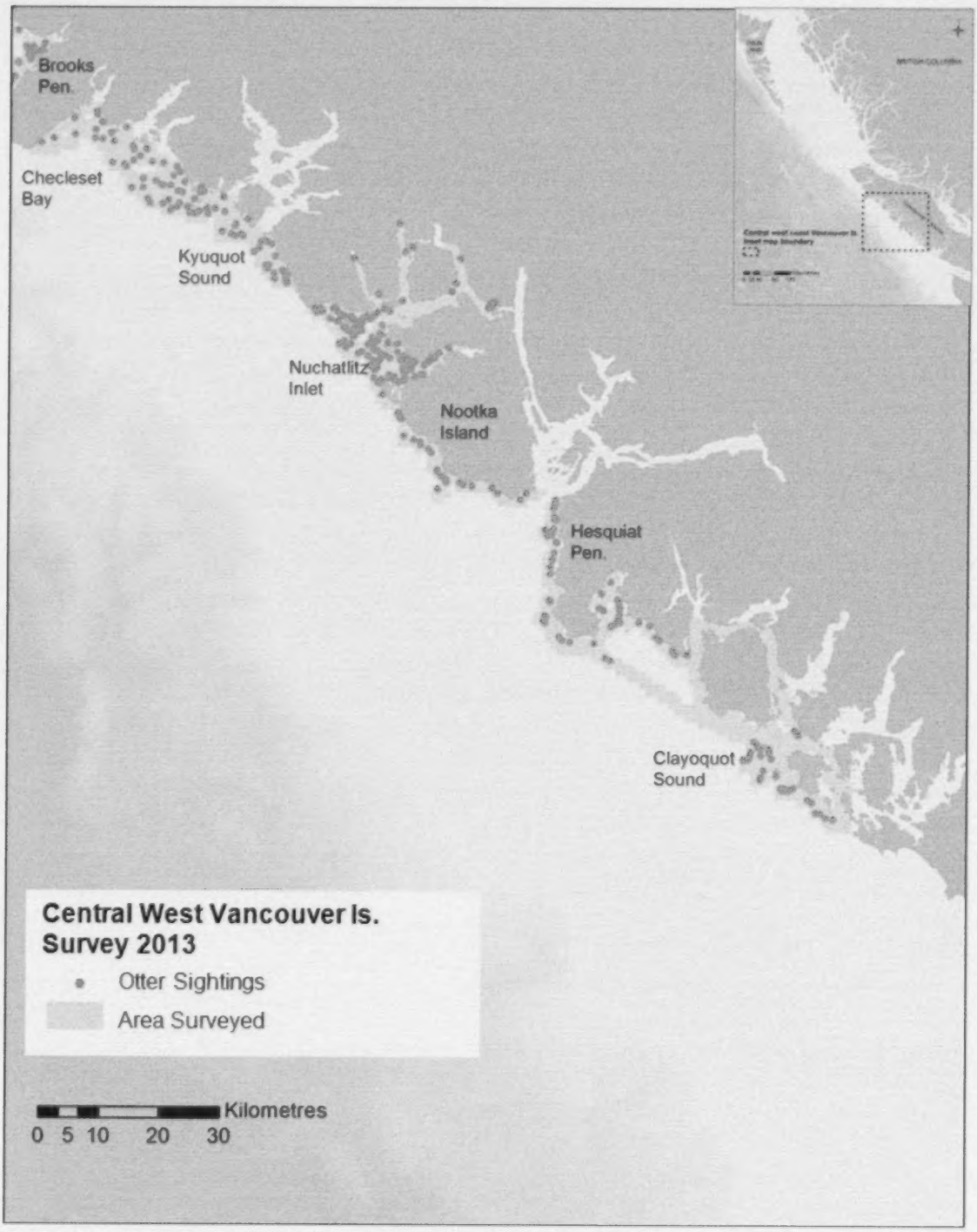


Figure 5. Distribution of sea otter sightings and survey effort on central west coast Vancouver Island in 2013.

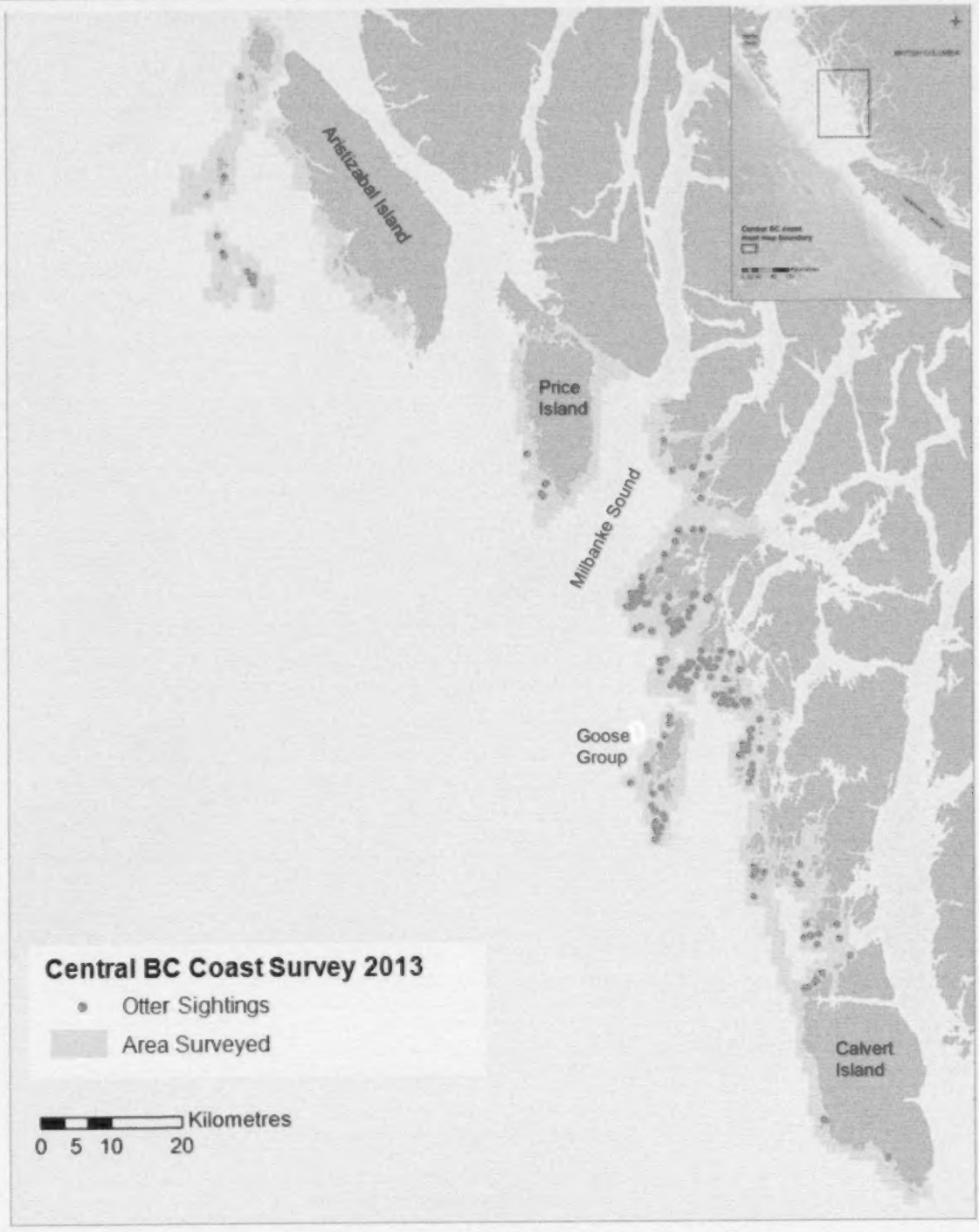


Figure 6. Distribution of sea otter sightings and survey effort on the central mainland coast in 2013.

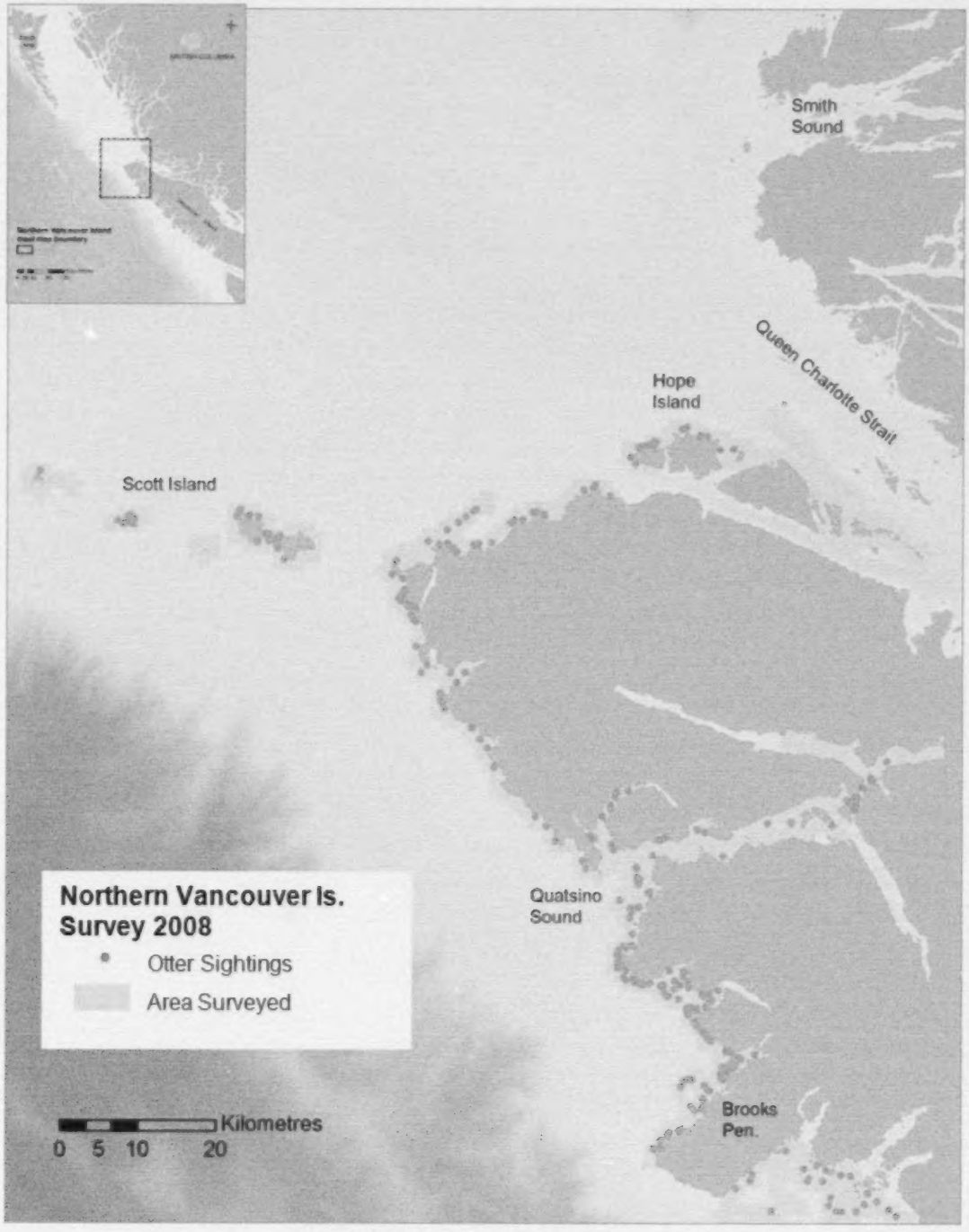


Figure 7. Distribution of sea otter sightings and survey effort on northern Vancouver Island in 2008.

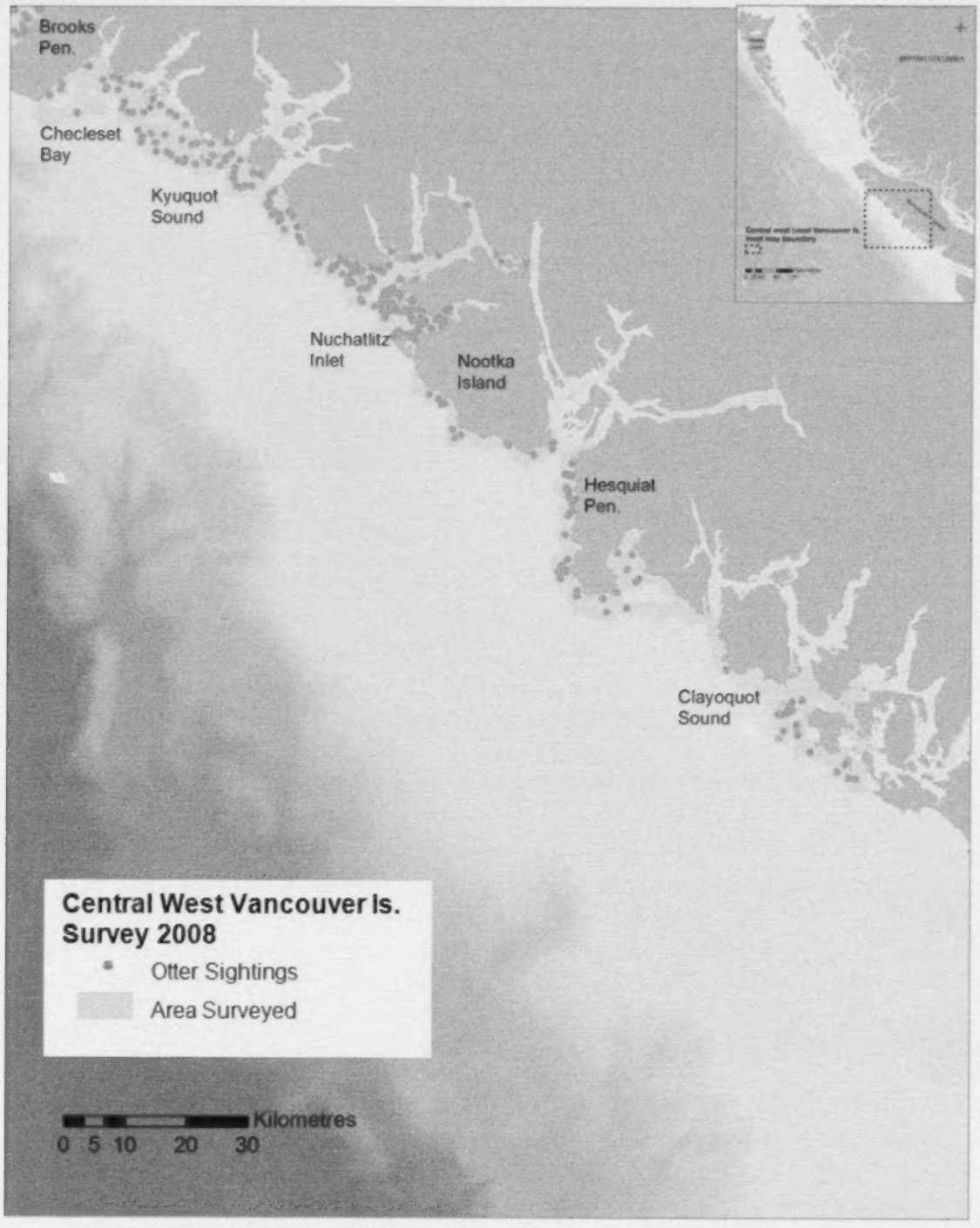


Figure 8. Distribution of sea otter sightings and survey effort on the central west coast of Vancouver Island in 2008.

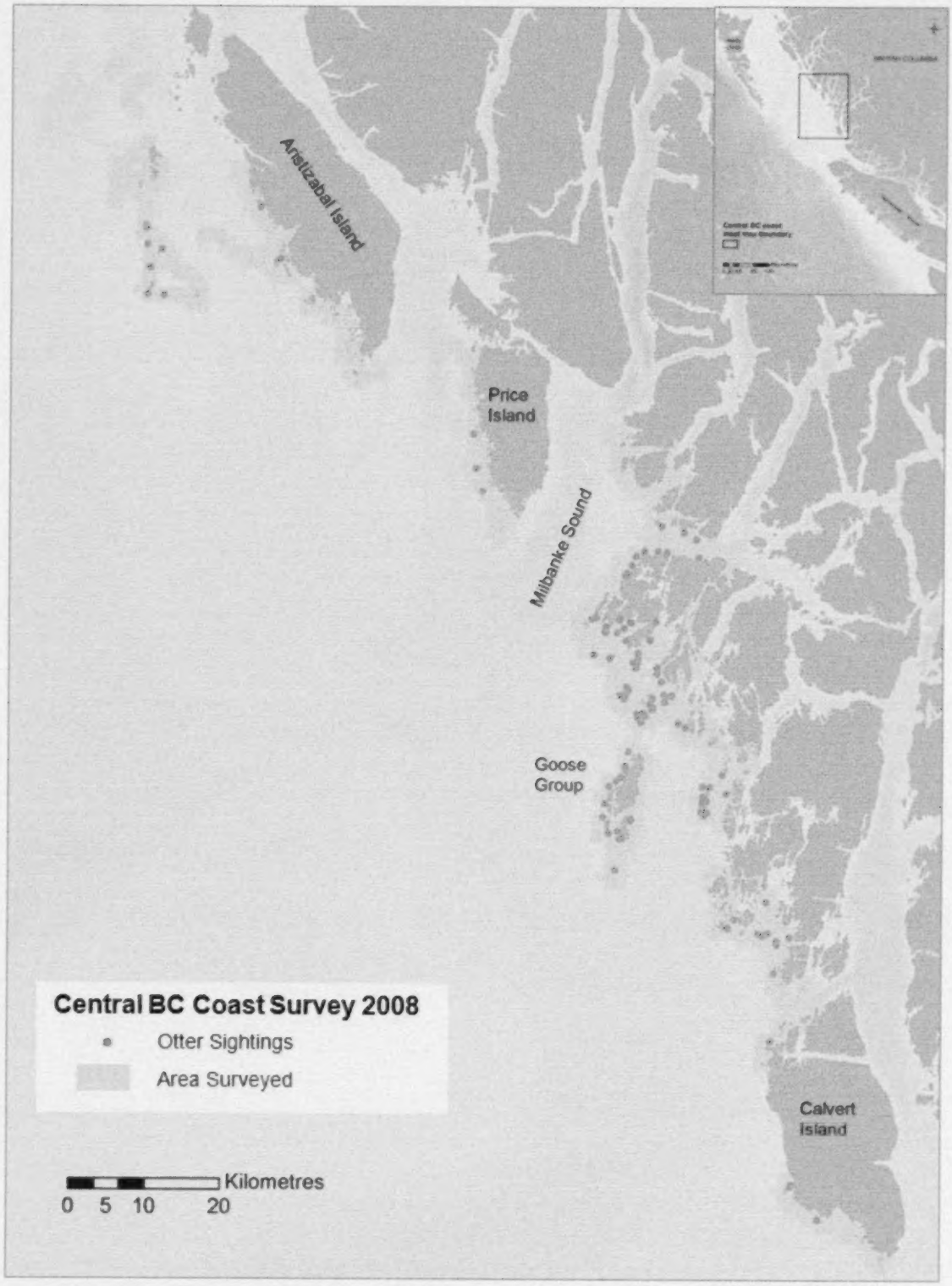


Figure 9. Distribution of sea otter sightings and survey effort on the central mainland coast in 2008.

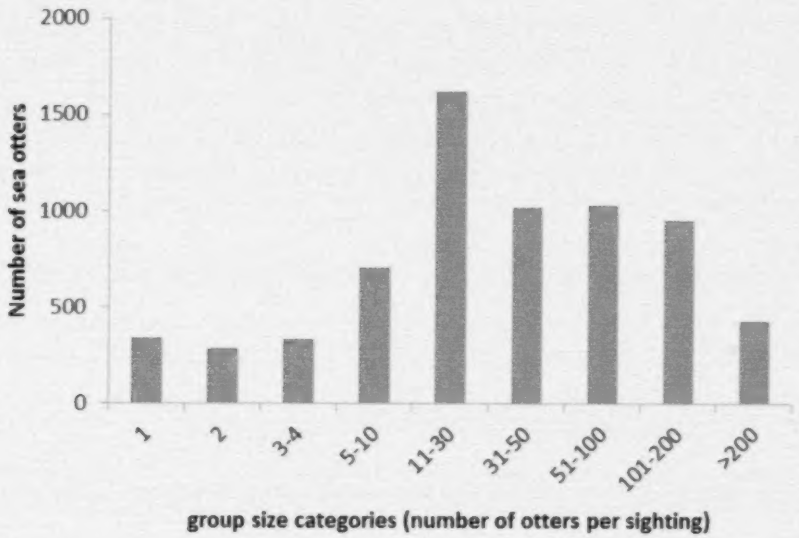
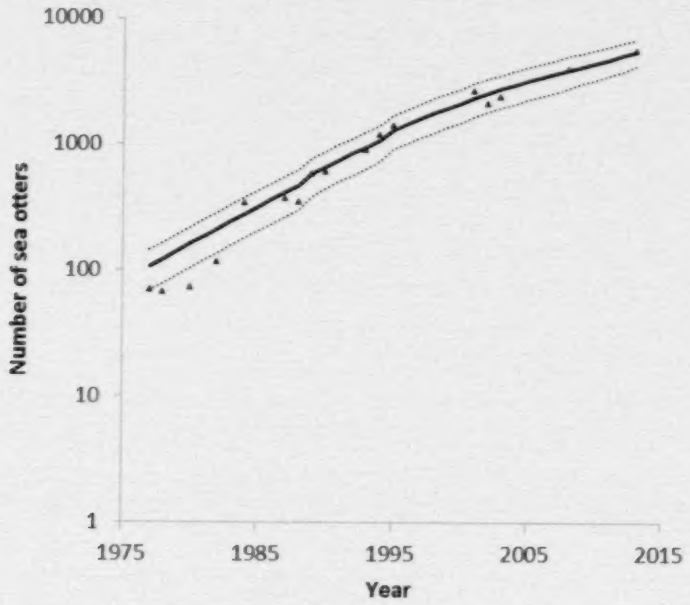


Figure 10. Number of sea otters by group sizes that comprised the 6,754 sea otters counted during surveys in 2013.

A.



B.

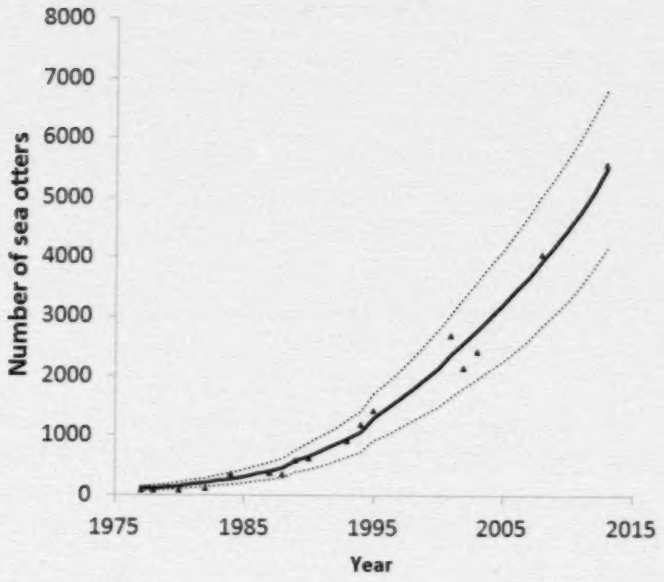
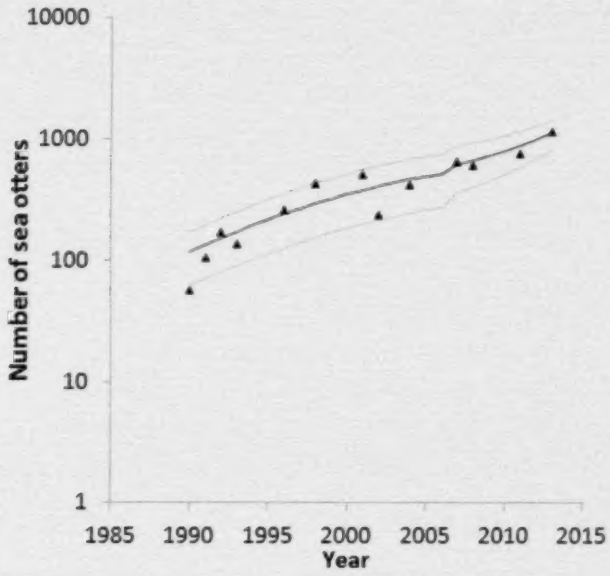


Figure 11. ***A.*** *Estimated population growth curve in the Vancouver Island region 1977 to 2013 on a log scale. Solid line represents the modelled expected values. Dotted line represents approximate 95% confidence intervals. Diamonds represent survey counts from years when all occupied survey segments were surveyed.* ***B.*** *Growth curve and 95% confidence intervals and survey count on an ordinal scale.*

A.



B.

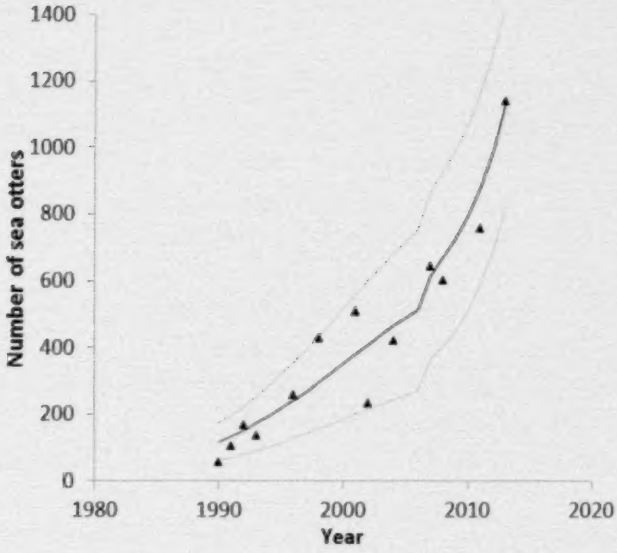


Figure 12. ***A.*** *Estimated population growth curve on the central mainland coast region 1990 to 2013 on a log scale. Solid line represents the modelled expected values. Dotted line represents approximate 95% confidence intervals. Diamonds represent survey counts from years when all occupied survey segments were surveyed.* ***B.*** *Growth curve and 95% confidence intervals and survey count on an ordinal scale.*

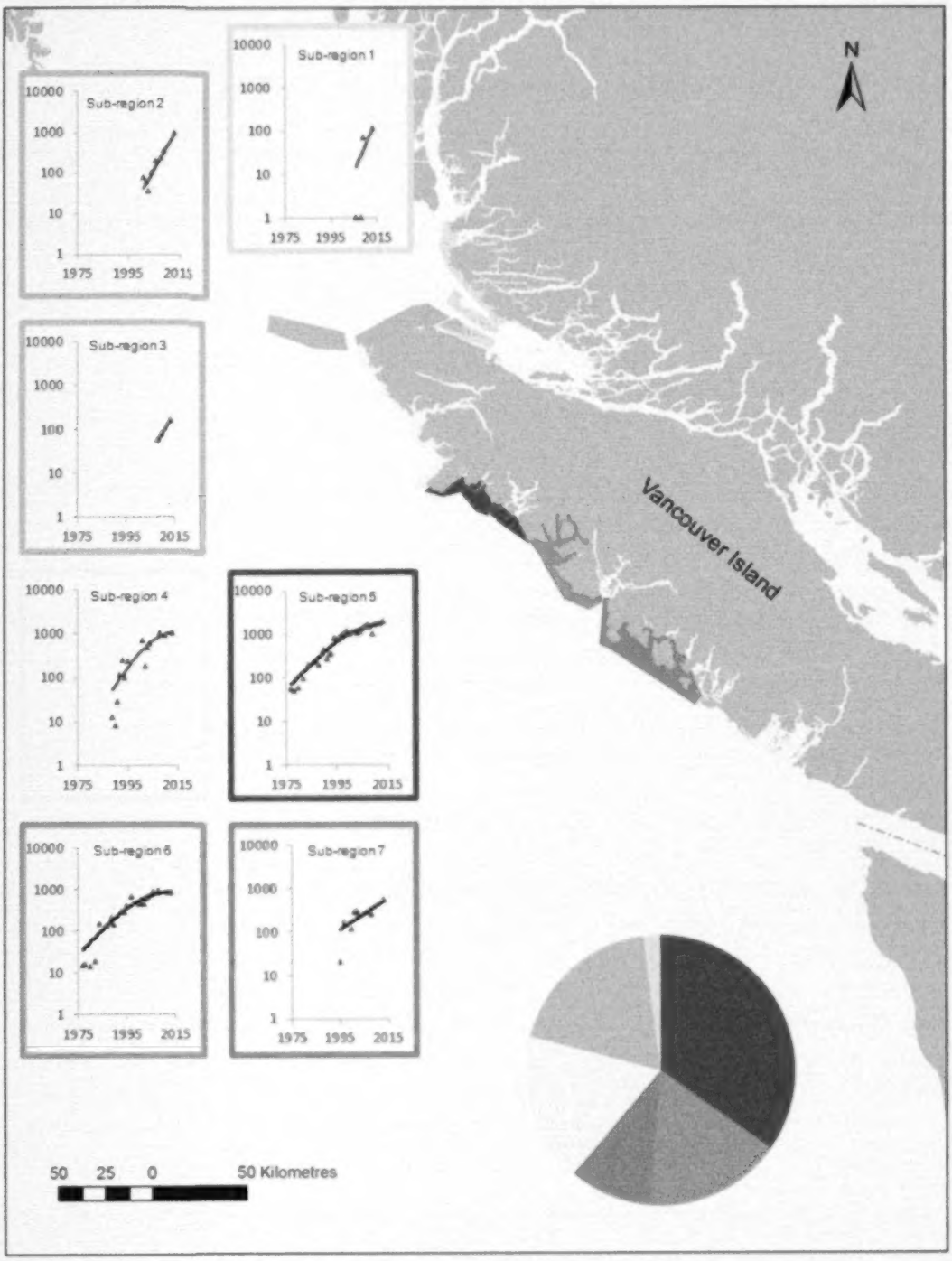


Figure 13. Estimated growth trends in the Vancouver Island region. Inset graphs show growth curves by subregion, either logistic or exponential (on a log scale) fitted to sea otter survey data. Inset pie chart gives the proportions of the 2013 count (5,612 sea otters) by sub-region.

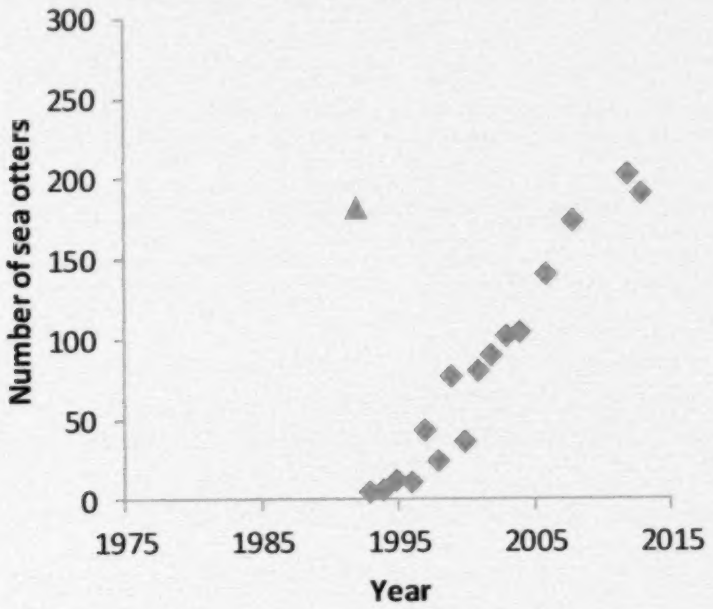


Figure 14. Pattern of colonization and growth observed in the Catala Island segment following initial range expansion by a raft of males in 1992 (red triangle). Diamonds represent counts in subsequent years which were predominantly females and pups.

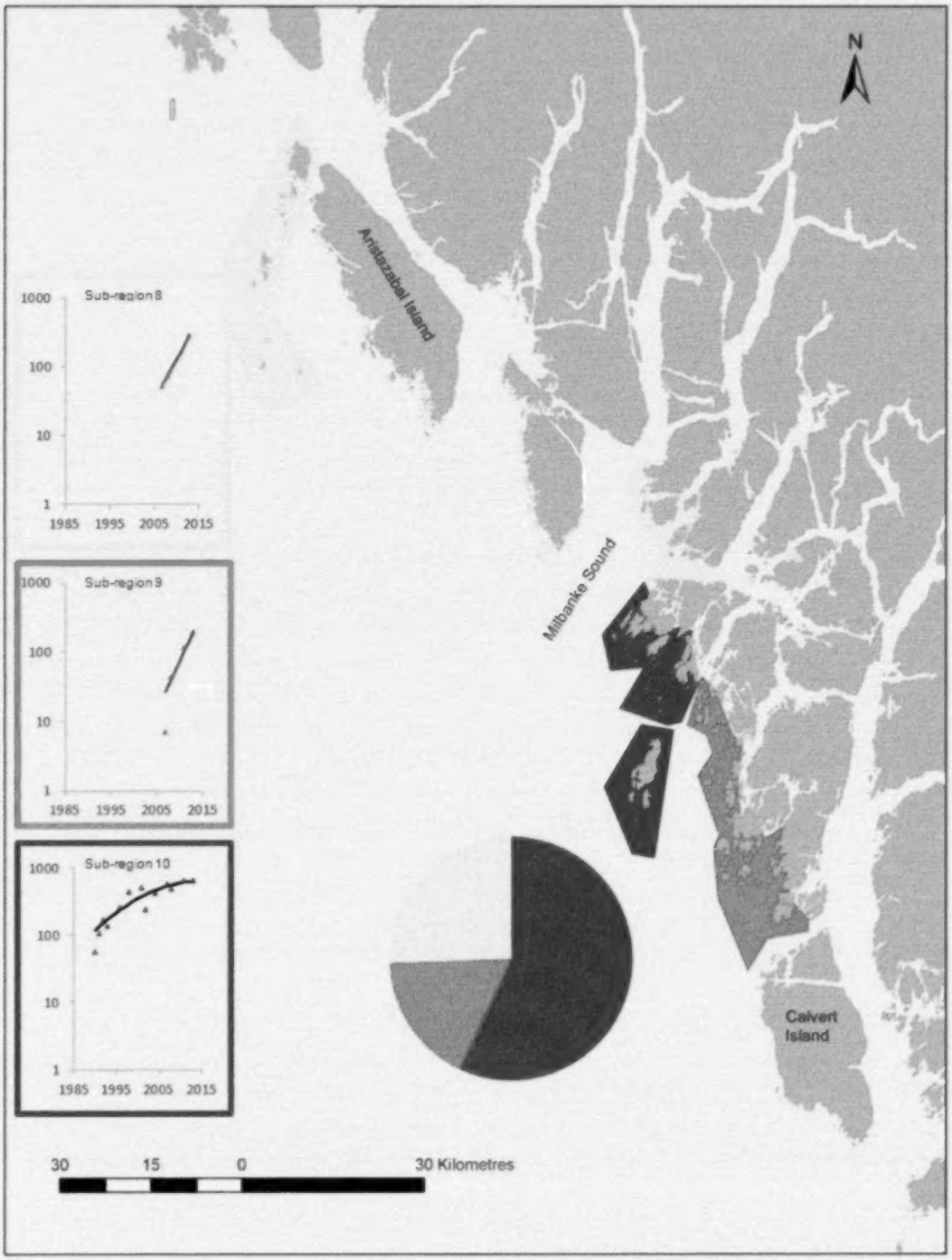


Figure 15. Estimated growth trends in the central mainland coast region. Inset graphs show growth curves by subregions either logistic or exponential (on log scale) fitted to sea otter survey data. Inset pie chart gives the proportions of the 2013 count (1,142 sea otters) by sub-region.